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EVOLUTIONARY TRENDS IN THE ATRIPLEX PROSTRATA GROUP OF SCANDINAVIA

BY MATS GUSTAFSSON

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AV

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Akademisk avhandling som för avläggande av filosofie doktorsexamen vid Matematisk-Naturvetenskapliga Fakulteten vid Universitetet i Lund kommer att offentligen försvaras å föreläsningssalen vid Institutionen för Systematisk Botanik, torsdagen den 15 maj 1975 klockan 10.00.

Lund 1975

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TO THE MEMORY OF GÖTE TURESSON

WHO INITIATED THE WORK

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The thesis is based on the following papers:

Gustafsson, M. 1973 a. Evolutionary trends in the Atriplex triangularis group of Scandinavia. I, Hybrid sterility and chromosomal differentiation. -- Bot. Notiser 126: 345--392.

-- 1973 b. Evolutionary trends in the Atriplex triangularis group of Scandinavia. II. Spontaneous hybridization in relation to reproductive isolation. -- Bot. Notiser 126: 398--416.

-- 1974. Evolutionary trends in the Atriplex triangularis group of Scandinavia. III. The effects of population size and introgression on chromosomal differentiation. -- Bot. Notiser 127: 125--148.

-- 1975. Evolutionary trends in the Atriplex prostrata group of Scandinavia. IV. Taxonomy and morphological variation. -- Opera Bot. (in manuscript).

DELIMITATION OF THE A. PROSTRATA GROUP

The A. prostrata group comprises halophytic species with green, rhombic to hastate lower leaves and with bracteoles united up to the middle at most. In Scandinavia five taxa are recognized, viz. A. glabriuscula Edmondst., A. longipes Drej. ssp. longipes, A. longipes Drej. ssp. praecox (Hülph.) Turess., A. prostrata DC. ssp. prostrata and A. prostrata DC. ssp. calotheca (Rafn) M. Gust. comb. nov. All the taxa are annuals and diploids with the chromosome number 2n=18.

MORPHOLOGY AND MORPHOLOGICAL VARIATION

The intrapopulational variation is particularly pronounced in A. prostrata ssp. prostrata and most populations are highly polymorphic in characters such as habit, height, size and shape of leaves and bracteoles. In the other taxa, a wide intrapopulational variation can be observed in some populations and a relatively narrow range of variation in others. In both A. longipes ssp. longipes and A. prostrata ssp. prostrata morphological differences between populations are rather small and the degree of over-

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lapping extensive. In A. glabriuscula, A. longipes ssp. praecox and A. prostrata ssp. calotheca morphological differences exist between some populations but not between others. Many characters show a high degree of overlapping between taxa. The diagnostic characters are limited to the shape of leaves and bracteoles. However, other biological differences also exist, for instance rate of vegetative development, flowering time, length of the protogynous stage, floating capacity of the bracteoles enclosing the seed, ecological preferences, and population structure.

CULTIVATION EXPERIMENTS

Cultivation experiments have been carried out in all taxa, but primarily in A. prostrata ssp. prostrata. Characters used for distinguishing taxa within the polymorphic A. prostrata ssp. prostrata, such as height and leaf size but to some extent also habit and shape of leaves, are highly modificative.

HABITAT AND DISTRIBUTION

All the taxa inhabit seashores of different types, A. prostrata ssp. prostrata also occurring on waste ground. A. glabriuscula and A. prostrata ssp. calotheca are mainly distributed in the southwestern parts of Scandinavia, A. longipes ssp. longipes in the southern parts, A. longipes ssp. praecox in the Baltic area and in the northern parts of Norway, while A. prostrata ssp. prostrata is distributed throughout the whole of Scandinavia. The present patterns of distribution indicate that A. longipes ssp. praecox is of Arctic origin, while the other taxa have probably reached Scandinavia from the southwest.

POPULATION STRUCTURE

Most of the populations of A. longipes ssp. longipes, A. prostrata ssp. prostrata and ssp. calotheca investigated are made up of a

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large number of individuals, about 2/3 of these populations being large or very large, i.e. comprising more than 1,000 individuals. The majority of populations of A. glabriuscula are of medium size, some large, i.e. they comprise more than 300 individuals. By contrast, most populations of A. longipes ssp. praecox are small or very small the number of individuals usually varying between 1 and 300.

BREEDING SYSTEM

All the taxa are monoecious and highly self-fertile. A. longipes has a relatively long period of protogyny, while A. glabriuscula and A. prostrata are virtually not protogynous. Protogyny favours cross fertilization in A. longipes. In the other taxa the degree of self fertilization seems to be high, even dominant. The pollen grains are probably dispersed by the agency of wind.

GERMINATION

Experiments on germination indicate that seed samples of "pure" taxa germinate to a high degree (usually 60—100 %). However, for successful germination the seeds need at least a short period of dormancy, and in addition the temperature must fluctuate above and below zero.

FERTILITY AND MEIOSIS

The frequency of plants with reduced male fertility (less than 90 % stainable pollen) has been investigated in 6 populations of A. glabriuscula, 16 populations of A. longipes ssp. longipes, 14 populations of A. longipes ssp. praecox, 19 populations of A. prostrata ssp. prostrata and 6 populations of A. prostrata ssp. calotheca. The following results were obtained: 1. Plants with reduced fertility occur most commonly in populations of A. longipes ssp. praecox (about 20 % of the material), less commonly in the other taxa (6—9 %). 2. The frequency of plants with reduced fertility varies within populations of all taxa.

3. In A. longipes ssp. praecox plants with reduced fertility are commoner in small populations than in medium-sized to large ones. 4. In populations of A. longipes ssp. longipes and A. prostrata ssp. prostrata affected by introgression, the frequency of plants with reduced fertility is higher than in non-introgressive populations.

In all plants meiotically investigated, reduced fertility is to a great extent caused by the formation of bridges and laggards at anaphase I. Bridge-formation is probably due to heterozygosity for paracentric inversions.

REPRODUCTIVE ISOLATION AND HYBRIDIZATION

On the whole, the reproductive isolation between taxa is relatively small, but varies in different regions of Scandinavia. In the Baltic region, A. longipes ssp. praecox is ecologically isolated from A. longipes ssp. longipes and A. prostrata ssp. calotheca, and seasonal isolation exists between A. longipes and the other taxa. In W Scandinavia the seasonal isolation is only partial due to the fact that the flowering periods differ somewhat although overlapping occurs. In the northern parts of Norway the taxa flower simultaneously. Consequently hybridization and the occurrence of hybrid derivatives are relatively rare in the Baltic region, but relatively common in W Scandinavia and N Norway. Although reproductive isolation is rather weak the taxa remain relatively distinct.

The investigation of cultivated hybrid progenies derived from seeds produced by natural hybrids indicates the following: 1. Hybrid seeds usually germinate poorly compared with seed samples of "pure" taxa. 2. Plants with reduced fertility occur in all hybrid progenies, but this is most pronounced in A. glabriuscula x A. prostrata ssp. prostrata, and in A. longipes ssp. longipes x A. prostrata ssp. prostrata. 3. Morphological segregation towards the pa-

rent species is not necessarily combined with restoration of fertility.

INTROGRESSION

Introgression occurs between most taxa, but is most frequent between A. longipes and A. prostrata ssp. prostrata, and between A. prostrata ssp. prostrata and ssp. calotheca. This has lead to: 1. The transfer of morphological traits from one taxon to another. 2. An increased frequency of plants with reduced fertility. 3. In A. prostrata ssp. prostrata reduced fertility is commoner in F_1 progenies of crosses between non-introgressive populations than of crosses between introgressive populations.

CROSSING EXPERIMENTS

In the A. prostrata group crosses are easily performed, but seeds of intraspecific as well of interspecific crosses germinate poorly. The germination is low compared with that of seed samples of "pure" taxa. The majority of the hybrids are well-developed vegetatively and the seed-setting is good.

The aims of the crossing experiments have been to investigate: 1. Crosses between isolated populations within taxa, with special reference to morphological differences and geographical distance between the parent populations crossed in relation to hybrid fertility. 2. The mode and strength of internal barriers in crosses between taxa. 3. The relation between hybrid fertility and size of parent populations crossed. 4. The relation between chromosomal alterations and reduced hybrid fertility.

F_1 fertility in crosses within taxa

Interpopulational crosses have been carried out within A. longipes ssp. longipes (48 crosses), ssp. praecox (37) and A. prostrata ssp. prostrata (88). The following results were obtained: 1. Reduced fertility is common in crosses within A. longipes ssp. praecox, where about 80 % of the crosses have fertility values of less than 80 % stainable

pollen. Reduced fertility is less pronounced in crosses within A. longipes ssp. longipes and A. prostrata ssp. prostrata, where the corresponding figures are 15 % and 28 % respectively. 2. In A. longipes ssp. longipes and ssp. praecox little or no correlation exists between geographical distance separating parent populations and the fertility of their hybrid offspring. 3. In all three taxa there is virtually no correlation between hybrid fertility and morphological diversities between the parent populations crossed.

F_1 fertility in crosses between taxa

In some combinations the number of crosses is small, due to experimental difficulties. The results indicate, however, that the fertility of most crosses entailing A. longipes ssp. praecox is reduced (mean values about 70 % stainable pollen), while crosses between the other taxa are generally highly fertile (about 85—90 %). Baltic populations of A. longipes ssp. praecox have been crossed with populations of A. longipes ssp. longipes from the Baltic region, W Sweden and Denmark respectively. Reduced hybrid fertility is most pronounced in the Baltic region, where the taxa occur sympatrically. Selection for a crossing barrier has probably taken place in this region.

Fertility and morphological variation in F_2 progenies

Eighty-nine F_2 progenies were raised by selfing F_1 hybrids representing different crossing combinations at different levels of fertility. In most crosses between taxa there is a range from almost completely fertile F_2 hybrids to hybrids with varying degrees of reduced fertility. Restoration of fertility seems to occur more readily in intraspecific than in interspecific crosses. Analysis of F_2 progenies indicates that most morphological characters are inherited independant of one another and that at least some traits are conditioned by more than one pair of genes.

The effects of population size on hybrid fertility

The degree of reduced fertility in crosses between populations of differ-

ent size has been investigated in intraspecific as well as in interspecific combinations. The results show that crosses with small populations of A. longipes ssp. praecox have a much higher frequency of reduced fertility than crosses between medium to large populations of ssp. praecox and of the other taxa.

Meiotic behaviour in hybrid plants

Meiosis has been investigated in representatives of 42 intraspecific as well as interspecific crosses. At metaphase I nine bivalents are regularly formed. No multivalents have been observed, but univalents were observed in two crosses. At anaphase I the number of cells with visible disturbances is often rather high, but these are exclusively of two types, viz. bridges and laggards. Usually single bridges have been observed, but two bridges have been observed occasionally. The correlation between the frequency of bridges formed at anaphase I and hybrid fertility is high (r=0.72), the lower the fertility, the higher the ferquency of bridges. In the A. prostrata group all information indicates that formation of bridges at anaphase I is probably due to heterozygosity for paracentric inversions. Analysis of F_2 progenies indicates that in several crosses reduced fertility is caused by two small inversions rather than by a single large one.

INVERSION POLYMORPHISM

Investigations of fertility in natural populations, hybrid fertility and meiotic behaviour indicate that polymorphism for paracentric inversions is most pronounced in small populations of A. longipes ssp. praecox, less so in medium to large praecox populations and in A. prostrata ssp. prostrata, and is of little significance in the other taxa.

EVOLUTION

The extent and rate of intra- and interspecific differences in the A. prostrata group in Scandinavia is apparently to a great extent based on

evolution that took place before the last glaciation or in ice-free areas during the last glaciation. The present pattern of variation thus depends on the origin of the Scandinavian material and the different migratory routes, as well as on evolution, adaptation and gene flow within Scandinavia after the last glaciation, i.e. within the last 10,000 years.